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18. The spectrograph collects the radiation from an area of 3 μm in diameter of the sample through a pinhole with 50 μm in diameter. The temperature gradient over this area is only a few degrees. The error bars in Fig. 2 reflect the laser power fluctuation (root mean square is less than <0.5%). We followed the method suggested by Boehler *et al.* (*2*) in using a ruby crystal on the top of the sample as the isolator. The use of crystals eliminates the possibility of any significant reaction with the sample. In particular at the subsolidus temperature range of our study, reaction between the iron and the ruby was not a problem. A circular area with diameter of 3 μm was sampled by the spectrograph to get one pressure value; this method reduces errors in pressure determination resulting from the presence of a pressure gradient in the chamber. The pressure was determined at room temperature. Following the discussion by D. L. Heinz [*Geophys. Res. Lett.* **17**, 1161 (1990)], we added 7% to the observed value to account for the thermal pressure. Before measurement, we heated a spot with the laser to relax the sample assemblage mechanically The pressure usually dropped by up to 16% of the initial unrelaxed value. The pressure drop was almost linear and could be stabilized by repeated heating. The errors in pressure shown in Fig. 2 are based on a value of 7% and thus accounts for not only point to point variation within the heated area of the sample (within 1%) and any misjudgment of the thermal pressure
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21. Although our study was not concerned specifically with melting, we used melting data in summarizing the iron phase relations. Boehler *et al.* (*2*) found that iron melts at substantially lower pressures than did Williams *et al.* (*4*). This has led to considerable arguments over the use of solid pressure medium and the possibility of reaction between the solid and iron. However, Jeanloz (*1*) did not find any reaction in his studies at least to a pressure of 40 GPa. The melting data of Shen *et al.* (*6*), Boehler *et al.* (*2*), and Liu and Bassett (*10*) do match well and, with increasing temperature, begin to deviate systematically from the data of Williams *et al.* (*4*). Therefore, we have adopted the data from Boehler *et al.* (*2*).
22. We thank R. Boehler, Y. Fei, and H. K. Mao who helped us in establishing our laboratory and sharing their experience with us. Discussions with A. Belonoshko and O. Anderson were useful. The work has been supported financially by grants from the Swedish Natural Science Research Council and Wallenberg's Foundation.

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Net Exchange of CO_2 in a Mid-Latitude Forest

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The eddy correlation method was used to measure the net ecosystem exchange of carbon dioxide continuously from April 1990 to December 1991 in a deciduous forest in central Massachusetts. The annual net uptake was 3.7 ± 0.7 metric tons of carbon per hectare per year. Ecosystem respiration, calculated from the relation between nighttime exchange and soil temperature, was 7.4 metric tons of carbon per hectare per year, implying gross ecosystem production of 11.1 metric tons of carbon per hectare per year. The observed rate of accumulation of carbon reflects recovery from agricultural development in the 1800s. Carbon uptake rates were notably larger than those assumed for temperate forests in global carbon studies. Carbon storage in temperate forests can play an important role in determining future concentrations of atmospheric carbon dioxide.

Combustion of fossil fuel releases ~5.5 Gt of carbon per year (1 Gt = 10^9 metric tons) to the atmosphere (*1*), with an additional 1 to 2 Gt $year^{-1}$ released from tropical deforestation (*2*, *3*). About 2 Gt $year^{-1}$ is removed by the ocean (*4*, *5*) and 3 Gt $year^{-1}$ accumulates in the atmosphere (*6*). The balance, 1 to 2 Gt $year^{-1}$, is often presumed (*6*, *7*) to be stored by aggrading temperate forests. However, available estimates (*3*, *8*) indicate that the rates of net carbon uptake by temperate forests are insufficient to balance the global carbon budget.

Mean rates for carbon uptake by aggrading temperate forests have been estimated as 2.5 metric tons per hectare per year for 50 years after disturbance, near zero at longer times (*3*). Early models for global rates of carbon uptake assumed that temperate forests accrete carbon linearly with time during succession (*3*), with equilibrium carbon stocks estimated on the basis of allometric relations derived from a small number of destructive harvests (*9–11*) and with limited information on belowground components (*10*). Estimates of rates for carbon uptake by forests can be significantly refined if the eddy correlation technique is used to determine the net ecosystem flux (*12*), for time scales from hours to years. This method provides a direct measurement of annual net uptake as well as information on underlying ecosystem processes. However, eddy correlation studies have not been carried out for periods long enough to define seasonal or annual carbon exchange in forests (*13*).

In this report we present nearly continuous measurements of net ecosystem exchange (NEE) for CO_2 for 2 years in a regenerating temperate forest using the eddy correlation method. We determined hourly, daily, and seasonal net fluxes for the ecosystem for 1990 and 1991. Our study site was located at Harvard Forest, Petersham, Massachusetts (42.54°N, 72.18°W; elevation, 340 m), in a 50- to 70-year-old mixed deciduous forest (red oak, red maple, and white and red pine, with scattered individuals of yellow and white birch, beech, ash, sugar maple, and hemlock). The terrain was moderately hilly, ~95% forested, with the nearest paved roads >1 km away and small towns >10 km away.

We instrumented a tower to measure the exchange of CO_2 by eddy correlation at an altitude of 30 m, 6 m above the canopy (*14*). We computed the vertical flux from the covariance of fluctuations of vertical wind speed with CO_2 concentrations, averaged over 30 min (*14*, *15*), with special consideration of nighttime data (*16*). We obtained companion measurements of CO_2 concentrations sequentially (two cycles per hour) at 29, 24, 18, 12, 6, 3, 1, and 0.05 m, using an independent gas analyzer. The net exchange of CO_2 between the atmosphere and the vegetation plus the soil, the NEE (in kilograms of carbon per hectare per hour) is defined by

$$\mathrm{NEE} \equiv \phi_{soil} + \int_0^{30\ \mathrm{m}} (R_a - P)dz \qquad (1a)$$

where P is canopy photosynthesis, ϕ_{soil} is soil flux, and R_a is aboveground respiration. Our measurements of the eddy corre-

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lation flux at 30 m, F, and the vertical concentration profile provide a direct measurement of NEE,

$$\mathrm{NEE} = F + \frac{dC}{dt} \quad (1b)$$

where $c(z)$ is the CO_2 concentration at height z and

$$\frac{dC}{dt} \equiv \frac{d}{dt}\int_0^{30\ \mathrm{m}} c(z)dz$$

is the rate of change of CO_2 content between 0 and 30 m.

The NEE of CO_2 was positive (respiration exceeded assimilation) from fall through spring, except for warm intervals when photosynthesis by conifers (~25% of the canopy) and understory plants was observed. Carbon uptake increased dramatically in June after leaves emerged, peaked in July and August, and then declined in late September during leaf senescence (Fig. 1).

Ecosystem respiration (R) was determined from nighttime NEE; R increased with soil temperature measured at a depth of 5 cm (soil temperature T_s, see Fig. 2) according to

$$R = 0.32(\pm 0.07) + 0.075(\pm 0.008)\ T_s \quad (2)$$

$-2°C < T_s < 20°C$, where ± denotes 1σ. Chamber measurements at Harvard Forest (*14*) indicated that belowground respiration accounted for >80% of R, with much of the balance due to stem respiration. Values for R are similar to soil fluxes observed in a variety of temperate forests (*17, 18*). The annual integral for R, based on the use of hourly soil temperatures in Eq. 2, was 7.4 metric tons of carbon per hectare in 1991, slightly larger than obtained from a regression of soil flux against mean annual air temperature for a variety of forests (*18*) (6.5 metric tons per hectare per year at 7.5°C, the annual mean air temperature for Harvard Forest).

Carbon uptake increased systematically with incident photosynthetically active radiation (PAR) (Fig. 3A). Uptake was slightly less after noon than in the morning for a given PAR, indicating modest effects of water stress, carbohydrate status, elevated air or soil temperatures, or lower ambient CO_2. We fit hourly mean data to

$$\mathrm{NEE} = a_1 - \frac{a_2\mathrm{PAR}}{1 + a_3\mathrm{PAR}} \quad (3)$$

with $r^2 > 0.9$ (r is the correlation coefficient), $a_1 \approx R$, and the half-saturation value a_3^{-1} close to the mean daily maximum PAR, in most intervals. The marginal quantum yield as incident PAR approaches zero, a_2, gives the maximum quantum efficiency: low sun angles favor interception by leaves, and low light intensities mitigate limitation of photosynthesis by carboxylation enzymes and related factors. During midsummer, a_2 at Harvard Forest was 0.04 to 0.055, similar to a_2 in the Amazon forest (*19*) and slightly lower than the maximum quantum yield observed for C_3 plants in greenhouses [0.06 to 0.07 (*20*)] (Fig. 3B).

We may define the mean effective quantum efficiency ($\langle q_{\mathrm{eff}}\rangle$),

$$\langle q_{\mathrm{eff}}\rangle = -\frac{\int_{24\ \mathrm{hours}} [\mathrm{NEE} - R(T_s)]dt}{\int_{24\ \mathrm{hours}} \mathrm{PAR}\ dt} \quad (4)$$

as the number of CO_2 molecules fixed per day by the canopy per incident photon. Values of $\langle q_{\mathrm{eff}}\rangle$ in midsummer averaged 0.02, 40 to 50% of a_2. Climatic conditions had only slight influence on $\langle q_{\mathrm{eff}}\rangle$ (for example, the modest decline during dry weather in July 1990), indicating that $\langle q_{\mathrm{eff}}\rangle$ is a well-defined property of the ecosystem. Eddy correlation measurements of NEE for selected intervals, along with measurements of incident PAR and T_s, could provide sufficient data to parameterize $\langle q_{\mathrm{eff}}\rangle$ and R as functions of PAR and T_s in mesic forests. Annual net carbon storage could then be computed from climatological observations of PAR and T_s (*21*).

We measured the diurnal course of leaf CO_2 exchange under ambient light at two levels in the canopy. The leaf data were scaled to ground area on the assumption that observations at upper and lower levels represented 1 and 2 m^2 of leaf area for each square meter of ground, respectively (1 and 1.5 in September) (*22*); R, computed from Eq. 2, was added to the scaled leaf measurements for comparison with the tower data. The leaf measurements reproduced most features of the diurnal and seasonal changes observed in the tower data (Fig. 1), except for a tendency to underestimate photosynthesis at midday.

Harvard Forest took up 6 metric tons of carbon per hectare in the growing season and released 2 metric tons per hectare in the dormant period, both in 1990 and in 1991 (Fig. 4), implying a net ecosystem production (NEP) of 4 metric tons of car-

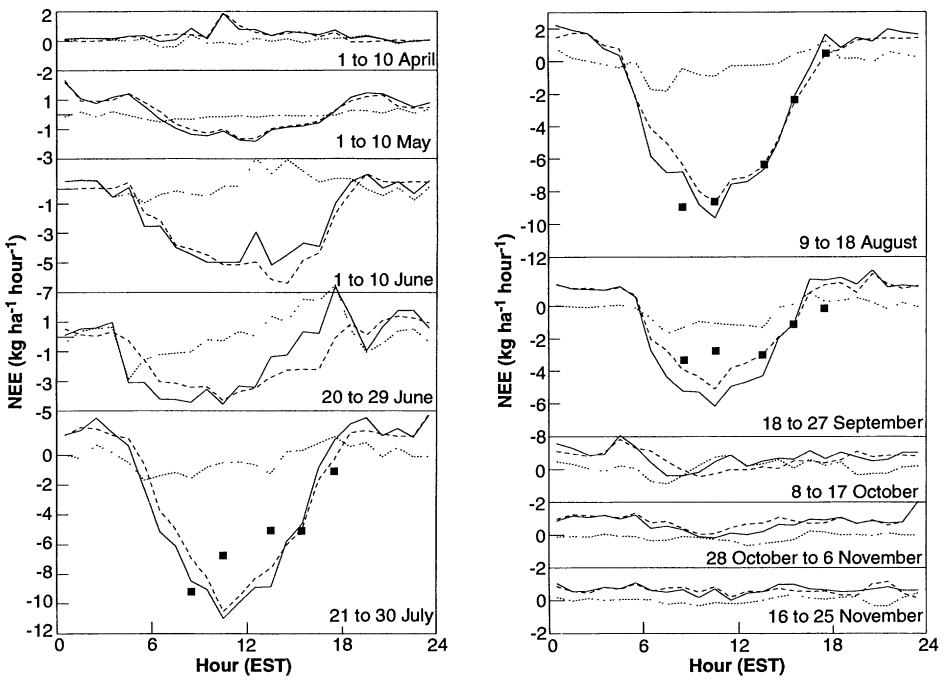

Fig. 1. Net ecosystem exchange (NEE) (——) and its components, F (flux at 30 m) (----) and dC/dt (····) (see Eq. 1), averaged by hour of the day (EST) for several 10-day periods in 1991. Solar noon is between 1130 and 1200 EST. The ■ symbols denote results from scaling leaf-level observations on canopy trees on 16 July, 22 August, and 28 September (see text).

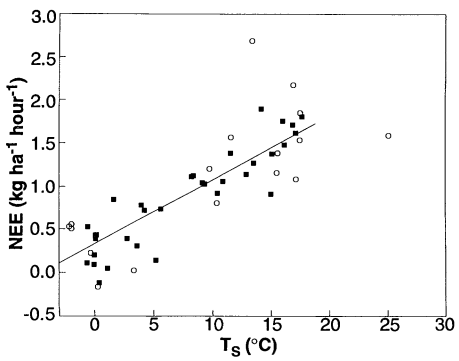

Fig. 2. System respiration between 2300 and 0300 (EST) (R), and soil temperature (T_s at a depth of 5 cm), averaged over 10-day periods, for 1990 (○) and 1991 (■). The linear least-squares fit (Eq. 2) accounts for 70% of the variance.

bon per hectare per year. Analysis of systematic errors (*16*) indicates a probable range for NEP of 3.5 to 4.0 metric tons per hectare per year. Stochastic errors associated with flux computations (*15*) and with absolute calibration introduce an additional uncertainty of ±15%, giving an overall range of 3.7 ± 0.7 metric tons per hectare per year. This value is consistent with recent allometric measurements of net growth at nearby plots (3.1 to 3.6 metric tons per hectare per year) (*23*), but larger than the 0 to 2.5 metric tons per hectare assumed in global carbon models (*3*, *8*) or the 0.5 metric ton per hectare inferred from silvicultural inventories of European forests (*9*). Gross ecosystem production, the annual assimilation of CO_2, was approximately 11.1 metric tons of carbon per hectare per year (the sum of NEP and heterotrophic and autotrophic respiration).

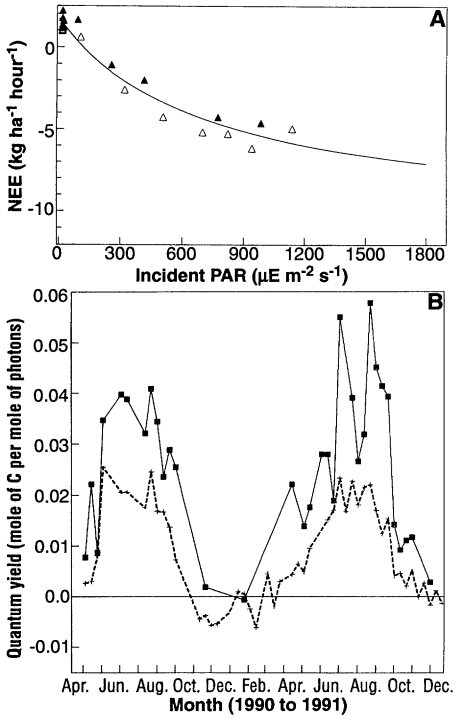

Fig. 3. (**A**) NEE plotted against PAR, for 18 to 27 September 1991; (▲) p.m.; (△) a.m. The equation for the fitted curve is NEE = 1.73 − 0.017 PAR/(0.0014 PAR + 1). (**B**) Seasonal variation of quantum yields for CO_2 fixation, obtained from tower data for 10-day periods with measurable photosynthetic uptake during daytime hours: (■), marginal quantum yield for PAR → 0 (a_2 in Eq. 3); (+) mean effective quantum efficiency, $\langle q_{eff} \rangle$ (Eq. 4).

Forest age and historical land use are expected to be major factors that regulate the rate of CO_2 uptake. Harvard Forest is heterogeneous, reflecting topography and past land use. Portions were cleared for agriculture between 1790 and 1830, then abandoned, reverting to forest by 1890 (*24*). Commercial logging in the 1920s and 1930s declined after a devastating hurricane in 1938. Eddy correlation measurements sample forest metabolism 100 to 500 m upwind of the tower during the day, with longer fetch at night (*25*). Our data show that *R* was highest when the fetch sampled poorly drained land northwest of the tower, an area used as a woodlot during the agricultural period, presently with patches of older hemlock (*24*). Canopy photosynthesis (NEE − *R*) did not show this asymmetry. We estimate that annual NEP for the former woodlot was about half of that for the more extensive area used previously for crops and pasture, indicating the importance of past land use, stand age, and soil characteristics in regulating net carbon storage.

Influx of nitrate and ammonium from the atmosphere, 10 kg of nitrogen per hectare per year (*26*), could stimulate growth, with associated uptake of as much as 2 metric tons of carbon per hectare per year if the additional biomass were primarily wood with a carbon/nitrogen ratio of ~200. However, nitrogen amendments to a nearby plot (*23*) indicated efficient microbial immobilization of nitrogen in these low-nutrient soils, implying that less than 10% of the net annual carbon uptake may be attributed to current rates of nitrogen deposition.

Ecosystem respiration rates (*R*) and quantum yields at Harvard Forest are similar to those in other temperate forests (*17–19*, *21*). The potential global area of temperate deciduous forests is 1.32×10^9 ha, ~50% cultivated at present (*27*). If the rate of carbon accumulation at Harvard Forest were representative, global uptake by temperate forests could exceed 2 Gt of carbon per year. Much of the currently forested area is managed for wood products or was formerly used for agriculture. If carefully managed, temperate forests could represent a significant global sink for CO_2. Boreal forests may also take up significant quantities of carbon: we observed a net uptake of 0.6 metric ton of carbon per hectare in Quebec [50°N, 72°W (*28*)] during July and August 1990, using the eddy correlation method.

The direct flux measurements presented here define NEE for time scales from 1 hour to several years, accounting fully for the storage of carbon above and below ground. The study demonstrates that eddy correlation observations may be carried out for long periods with sufficient resolution to integrate and partition carbon budgets for major ecosystems. We anticipate that similar investigations in a variety of ecosystems could advance our understanding of the global carbon cycle, by helping to develop and test mechanistic process models and remote-sensing algorithms and by providing data on the response of ecosystems to climatic variations.

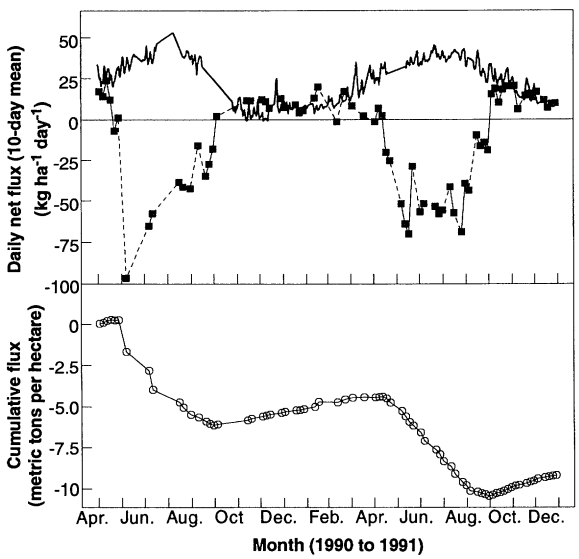

Fig. 4. (**Top**) NEE of CO_2 (averaged over 10-day periods ■) from April 1990 to December 1991. Broken lines indicate inadequate data for a 10-day interval. Daily values for *R* (Eq. 2) are shown in the upper curve. (**Bottom**) Cumulative net CO_2 exchange, arbitrarily starting at zero on 1 April 1990.

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14. Additional measurements included fluxes and concentrations of ozone, nitrogen oxides, and sensible heat. Wind speed and air density at 30 m were measured with a three-dimensional sonic anemometer; CO_2 and other gases were sampled through adjacent inlets and measured with the use of fast-response instruments at the base of the tower. Sensor calibration, time delay, and frequency response were determined automatically at 2- to 4-hour intervals by stepwise addition of standards to the inlet. Raw data were archived at 4 Hz. The flux F is given by $F = \langle w(t)[c(t) - \overline{c(t)}]\rangle$, where w is the wind speed perpendicular to the streamlines (*15*), c is the CO_2 concentration, t is time, $\langle\rangle$ denotes the average over 30 min, and the overbar represents the linear least squares fit versus time. Valid observations were obtained for 60% of the hourly intervals from April 1990 through 1992, with dropouts due to routine maintenance and data downloading, and notable gaps caused by lightning damage in July 1990 (20 days) and July 1992 (10 days) and by a malfunctioning tape drive in May 1991 (10 days). For 5 months when water was not trapped, we corrected air density for H_2O content as discussed by E. K. Webb, G. I. Pearman, and R. Leuning [*Q. J. R. Meteorol. Soc.* **106**, 85 (1980)]. In 1992 we measured belowground, stem, and leaf respiration using an array of ten chambers, continuously ventilated, sampled for several days at one site and moved weekly to cover ten locations around the tower.
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16. Observations at night were analyzed for errors associated with stratification, which shifts transport toward higher frequency turbulence and decouples air flow at the sensor from the forest. We corrected lack of response to high-frequency CO_2 fluctuations by computing, in each hourly interval, the error in the sensible heat flux (usually 4 to 10%) when the high-frequency temperature signal was filtered to simulate the effective bandpass of the CO_2 analyzer (*15*). We assessed errors due to decoupling by comparing NEE in stratified periods with data from well-coupled (windy) nighttime intervals (momentum flux $< -500\ cm^{-1}\ s^{-2}$), and with the sum of measurements (*14*) for belowground, stem, and leaf respiration. It appears that unstable temperature gradients usually maintain turbulent exchange between 0 and 30 m, and errors associated with decoupling are small: nighttime NEE may be underestimated in midsummer by 0 to 0.5 kg of carbon per hectare per hour, corresponding to a possible overestimate of the annual net uptake of 0 to 0.5 metric ton per hectare.
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Identification of the von Hippel–Lindau Disease Tumor Suppressor Gene

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A gene discovered by positional cloning has been identified as the von Hippel–Lindau (VHL) disease tumor suppressor gene. A restriction fragment encompassing the gene showed rearrangements in 28 of 221 VHL kindreds. Eighteen of these rearrangements were due to deletions in the candidate gene, including three large nonoverlapping deletions. Intragenic mutations were detected in cell lines derived from VHL patients and from sporadic renal cell carcinomas. The VHL gene is evolutionarily conserved and encodes two widely expressed transcripts of approximately 6 and 6.5 kilobases. The partial sequence of the inferred gene product shows no homology to other proteins, except for an acidic repeat domain found in the procyclic surface membrane glycoprotein of *Trypanosoma brucei*.

Von Hippel–Lindau (VHL) disease is a familial cancer syndrome that is dominantly inherited and that predisposes affected individuals to a variety of tumors. The most frequent tumors are hemangioblastomas of the central nervous system and retina, renal cell carcinoma (RCC), and pheochromocytoma. The minimum birth incidence of VHL disease is one in 36,000, penetrance is almost complete by 65 years of age, and median actuarial life expectancy is reduced to 49 years, with RCC being the most common cause of death (*1*). Genetically, the disease gene behaves as a typical tumor suppressor (*2*) as defined in Knudson's theory of human carcinogenesis (*3*).

By positional cloning strategies, we and others have delineated the VHL gene region at human chromosome 3p25-p26 (*4*) and have obtained a nearly complete genomic coverage in overlapping yeast artificial chromosomes (YACs) and cosmid-phage contigs (*5*) (Fig. 1). In parallel with the cloning efforts, we established a physical map of the region by pulsed-field gel electrophoresis and began looking for gross rearrangements affecting the region. These efforts resulted in the discovery of nested constitutional deletions in three unrelated VHL patients (*6*). This finding and the availability of cloned DNA provided rapid access to the VHL gene. We reasoned that